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Residence time and exposure time of sinking phytoplankton in the euphotic layer

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Abstract

The residence time of a sinking particle in the euphotic layer is usually defined as the time taken by this particle to reach for the first time the bottom of the euphotic layer. According to this definition, the concept of residence time does not take into account the fact that many cells leaving the euphotic layer at some time can re-enter the euphotic layer at a later time. Therefore, the exposure time in the surface layer, *i.e.* the total time spent by the particles in the euphotic layer irrespective of their possible excursions outside the surface layer, is a more relevant concept to diagnose the effect of diffusion on the survival of phytoplankton cells sinking through the water column.

While increasing the diffusion coefficient can induce both a decrease or an increase of the residence time, the exposure time in the euphotic layer increases monotonically with the diffusion coefficient, at least when the settling velocity does not increase with depth. Turbulence is therefore shown to increase the total time spent by phytoplankton cells in the euphotic layer.

The generalization of the concept of exposure time to take into account the variations of the light intensity with depth or the functional response of phytoplankton cells to irradiance leads to the definition of the concepts of light exposure and effective light exposure. The former provides a measure of the total light energy received by the cells during their cycling through the water column while the latter diagnose the potential growth rate.

The exposure time, the light exposure and the effective light exposure can all be computed as the solution of a differential problem that generalizes the adjoint approach introduced by Delhez et al. (2004) for the residence time. A general analytical solution of the 1D steady-state version of this equation is derived from which the properties of the different diagnostic tools can be obtained.

Key words: Residence time, mixed layer, exposure time, light exposure

1. Introduction.

The identification of the characteristic timescales of biological systems is central for the description and understanding of many aspects of their dynamics. Significant interactions can indeed only take place between processes sharing similar timescales. In particular, biological processes interact with the hydrodynamics processes with similar characteristic timescales which, in turn, imprint their characteristic length scales on the biological structures, a process sometimes called ecohydrodynamic adjustment (e.g Nihoul and Djenidi, 1991; Delhez, 1998; Ennet et al., 2000; Lessin and Raudsepp, 2007).

Many environmental phenomena strongly depend on hydrodynamic timescales. The occurrence of eutrophication problems can be related to the increased residence time in coastal waters (e.g. Wang et al., 2004; Lillebo et al., 2005; Painting et al., 2007). The ratio of the characteristic time scales of horizontal diffusion and the growth rate of phytoplankton cells is often regarded as an important factor for phytoplankton patchiness (e.g Malchow, 1996; Martin, 2003). According to many authors, the occurrence and magnitude of deep chlorophyll maxima depend not only on

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the light level at and below the pycnocline but also on the rate of nutrient replenishment from the deeper layers, the specific growth rate of the phytoplankton cells or the sinking rate of organic matter (e.g. Varela et al., 1994; Ediger and Yilmaz, 1996; Hodges and Rudnick, 2004).

The intensity of the vertical mixing plays a crucial role in the dynamics of primary production. According to the basic Sverdrup theory (Sverdrup, 1953; Lande and Yentsch, 1988; Huisman et al., 1999; Mann and Lazier, 2006), phytoplankton can thrive in the surface layer if the surface mixed layer is shallower than the so-called critical depth. This classical argument can be rephrased in terms of characteristic timescales with the blooming of phytoplankton depending on the ratio of the time scale of vertical mixing *vs* the net growth rate. If the mixed layer is too deep, phytoplankton cells will spend too much time in the darkness and the bloom will not start. On the contrary, cells will be able to develop if they receive enough light energy on average during their mixing through the surface layer. All together, it is important to understand how the hydrodynamics of the surface layer influence the level of irradiance received by photosynthetically active cells during their vertical mixing.

The issue is particularly complex for large phytoplankton species that can sink through the water column. In this case, not only the depth of the mixed layer is important but the strength and vertical structure of turbulence, the sedimentation rate and the rate of light attenuation with depth also seem critical for the net growth of the phytoplankton cells (e.g. Huisman and Sommeijer, 2002; Huisman et al., 2002).

It is generally believed that turbulence increases the residence time in the surface layer of settling particles and can therefore help sinking phytoplankton cells to remain for a longer time in the euphotic layer. This statement is however seldom supported by analytical proofs or numerical demonstrations. In previous studies, apparently conflicting conclusions were even presented by various authors (e.g. Lande and Wood, 1987; Maxey, 1987; Fung, 1993; Wang and Maxey, 1993; Ruiz, 1996; Franks, 2001; Deleersnijder et al., 2006a; Ross, 2006).

In this context, the aim of this manuscript is to use the concept of exposure time (e.g. Monsen et al., 2002; Delhez, 2006; Wolanski, 2007) to shed new light on the issue of the influence of turbulence on the time spent by sinking phytoplankton cells in the euphotic layer. In the last section, the concept of exposure time is also generalized to take into account the amount of light energy received by phytoplankton cells during their vertical mixing and provide therefore a better diagnosis of the influence of turbulence and sedimentation rate on the fate of phytoplankton cells in the euphotic layer.

2. Residence time in the euphotic layer.

The residence time of a water parcel, of a particle or of a phytoplankton cell in the euphotic layer can be roughly defined as the ‘the time taken by this water parcel, particle or phytoplankton cell to leave the euphotic layer’ (e.g. Bolin and Rhode, 1973; Takeoka, 1984; Delhez et al., 2004). This concept provides therefore and apparently obvious way to tackle the issue of whether turbulence allows negatively buoyant particles to remain for a longer time in the euphotic layer.

Strictly speaking, each particle has its own residence time. The residence time is of course a function of the depth at which the particle is released and starts its journey. In a turbulent flow, different particles will also follow different paths even if they are released in exactly the same conditions. Therefore, one should speak about the (statistical) distribution of the residence time, reflecting the individual histories of the particles (e.g. Bolin and Rhode, 1973; Takeoka, 1984; Delhez et al., 2004). Alternatively, the mean or any other relevant statistics of this distribution can be used. In the following, as in most previous studies, the focus will be on the mean value of the distribution.

The mean residence time of sinking particles has been evaluated by many authors. While some authors argue that turbulence increases the residence time in the surface layer (e.g. Fung, 1993; Ruiz, 1996; Deleersnijder et al., 2006a), others give the opposite conclusion (e.g. Maxey, 1987; Wang and Maxey, 1993; Franks, 2001). Using a random walk model, Ross (2006) computed the residence time in the surface mixed layer of a 1D vertical model of the water column. His numerical results suggest that turbulence increases the residence time. The opposite effect is however observed when a highly simplified representation of the vertical structure is used. Both behaviors are also obtained by Spivakovskaya et al. (2007) using the forward and backward versions of an Itô random walk model (LaBolle et al., 2000).

Lande and Wood (1987) provide a detailed analytical solution of the problem in the context of a two-layer model of the upper ocean. They consider a surface mixed layer of depth m on top of the thermocline and compute the residence

time in an euphotic layer that is assumed to be deeper than the surface mixed layer, *i.e.* $\ell > m$ where ℓ denotes the depth of the euphotic layer (Fig. 1). Although Lande and Wood (1987) also address a more general model of the water column, the most detailed results are given for a simplified two layer model in which the sinking rate and the turbulent diffusivity coefficient take the constant values (w_s, λ_s) and (w_b, λ_b) respectively in the surface mixed layer and in the thermocline. Since vertical mixing is reduced by stratification, one has in general $\lambda_b \ll \lambda_s$. The different settling velocities w_s and w_b account for the dependency of the vertical settling velocity on the density difference between the sedimenting particle and the surrounding water.

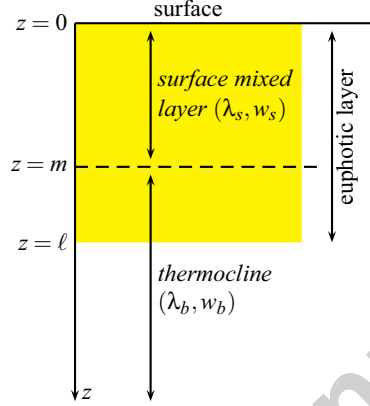


Figure 1: Schematic description of the two-layer model of the water column with piecewise constant profiles of the diffusivity coefficient and settling velocity.

According to Lande and Wood (1987), the expected time for a particle to reach the thermocline starting from a depth $z_0 \leq m$ in the mixed layer, *i.e.* the residence time in the mixed layer, is

$$\theta_m(z_0) = \frac{m - z_0}{w_s} - \frac{\lambda_s}{w_s^2} \left(e^{-z_0 w_s / \lambda_s} - e^{-m w_s / \lambda_s} \right) \quad (1)$$

(the vertical coordinate z is positive downward from the surface). The expected time for a particle to leave the euphotic layer starting at a depth $z_0 \in [m, \ell]$ in the thermocline is

$$\theta_\ell(z_0) = \frac{\ell - z_0}{w_b} + \frac{\lambda_b}{w_b^2} \left(e^{-(z_0 - m) w_b / \lambda_b} - e^{-(\ell - m) w_b / \lambda_b} \right) \left[\frac{\lambda_s w_b}{\lambda_b w_s} \left(1 - e^{-m w_s / \lambda_s} \right) - 1 \right] \quad (2)$$

Finally, the residence time in the euphotic layer for a particle initially located at depth $z_0 \leq m$ in the surface mixed layer is the sum of the time needed to reach the bottom of the surface mixed layer and the time to leave the euphotic layer from that depth, *i.e.*

$$\theta_\ell(z_0) = \theta_m(z_0) + \theta_\ell(m) \quad (3)$$

According to (1), the residence time in the surface layer θ_m is a decreasing function of the diffusivity coefficient λ_s in that layer. Because of diffusion, the particles hit the bottom of the mixed layer earlier than if they were simply advected vertically at the velocity w_s .

While all the results tabulated by Lande and Wood (1987) suggest an increase of the residence time in the euphotic layer as the vertical diffusivity in the surface mixed layer increases, the analytical expressions (2)-(3) describe a more complex behavior. Typical vertical profiles are shown in figure 2. In a large part of the range of variation of the parameters (but not all of it, not shown), the residence time is indeed an increasing function of λ_s for those particles released in the surface mixed layer. The residence time of particles released in the thermocline depends only weakly on λ_s , especially when $\lambda_b \ll \lambda_s$. The diffusion coefficient in the thermocline has a strong influence on the residence time for both particles initially located in the surface mixed layer and in the thermocline. An increase of λ_b generally

goes with a decrease of the residence time for particles initially located in the surface mixed layer. The residence time can then even become smaller than the advection time scale

$$\theta_\ell^\infty(z_0) = \begin{cases} \frac{\ell - m}{w_b} + \frac{m - z}{w_s} & z \leq m \\ \frac{\ell - z}{w_b} & z > m \end{cases} \quad (4)$$

that corresponds to the residence time of a settling particle when diffusion is neglected. For particles initially located in the thermocline, the residence time depends also in a non monotonic way on λ_b .

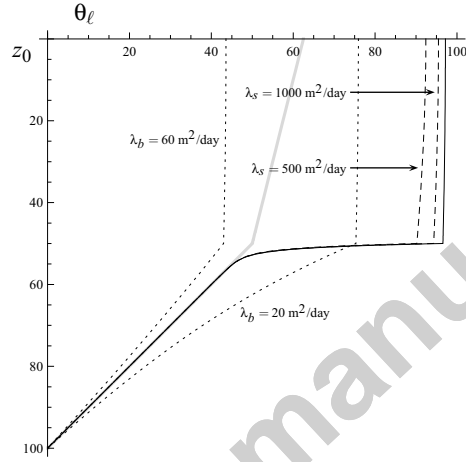


Figure 2: Vertical profiles of the residence time in the euphotic layer (in days) for $m = 50$ m, $\ell = 100$ m, $w_s = 4$ m/day, $w_b = 1$ m/day. The solid curve is used as a reference and is obtained with $\lambda_s = 2000$ m²/day and $\lambda_b = 1$ m²/day. These values are taken from Lande and Wood (1987). The dashed curves are obtained by varying the diffusion coefficient in the surface layer to $\lambda_s = 1000$ m²/day and $\lambda_s = 500$ m²/day. The dotted curves are obtained from the reference by increasing λ_b to 20 m²/day and 60 m²/day. The thick gray curve represents the advection time scale when diffusion is neglected. The residence time is sensitive to the turbulent diffusion coefficient in the thermocline. It can be smaller or larger than the advection time scale and depends in a non monotonic way on λ_b .

The results (1)-(3) can be recovered using the adjoint approach described by Delhez et al. (2004) and Deleersnijder et al. (2006a). The vertical profile of the mean residence time for $z \in [0, \ell]$ is then obtained as the solution of the differential problem

$$w \frac{d\theta}{dz} + \frac{d}{dz} \left(\lambda(z) \frac{d\theta}{dz} \right) + 1 = 0 \quad (5)$$

$$\lambda(z) \frac{d\theta}{dz} \Big|_{z=0} = 0 \quad (6)$$

$$\theta(\ell) = 0 \quad (7)$$

It should be mentioned that the hypothesis (7) used to derive the expressions (1)-(3) is not always acceptable. For instance, in the limit case when both the sinking velocity w_b and the eddy diffusivity λ_b vanish in the thermocline, the residence time cannot be zero at the bottom of the euphotic layer since particles released in the euphotic layer have then no way to leave this layer and remain there for ever. Even more delicate is the singular behavior of the residence time (1)-(3) when the diffusion coefficient vanishes in the thermocline, which is detailed in appendix A. In the broader context of a depth-varying eddy diffusivity profile, Deleersnijder et al. (2006b) have also shown that the residence time can take a non zero value at the bottom of the surface layer if the eddy diffusivity decreases rapidly to zero as the thermocline is approached from above.

3. Exposure time in the euphotic layer.

If one excepts the peculiar and highly idealized case when the diffusion coefficient is zero in the thermocline, the residence time is zero at the bottom of the euphotic layer, as in figure 2. This reflects the definition of the residence time at a depth z as the (mean) time needed for a particle released at that depth to reach the bottom of the euphotic layer *for the first time*. This definition, leading to (1)-(3), is inherited from the classical mathematical theory of random walk on the lattice points of ordinary Euclidean space (e.g. Spitzer, 2001). In the water column model considered here, the residence time is therefore zero at the bottom of the euphotic layer.

When computing the residence time numerically, the particles reaching the boundary of the control domain in which the residence time is evaluated are discarded as soon as they touch the boundary of this control domain (e.g. Delhez et al., 2004; Ross, 2006; Delhez, 2006). This approach is not fully appropriate when the aim is to quantify the effect of diffusion on the survival of phytoplankton. The cells leaving the euphotic layer at some time can indeed re-enter the euphotic layer at a later time – sometimes vary rapidly – because of vertical mixing, or in a more general context, because of particular upwelling events. Therefore, the exposure time in the surface layer, *i.e.* the total time spent by the particles in the euphotic layer irrespective of their possible excursions outside the surface layer (Delhez et al., 2004; Delhez and Deleersnijder, 2006; Wolanski, 2007), is a more relevant concept than the residence time.

The difference between the residence time and the exposure time is explained schematically in Fig. 3 using hypothetic trajectories of particles. While the residence time of a particle is the time needed to reach the bottom of the euphotic layer for the first time, the exposure time of that same particle is the sum of all the time intervals during which the particle is in the euphotic layer.

This difference between the residence en exposure times is also often introduced when studying the flushing of tidal estuaries, although the name ‘exposure time’ is seldom used explicitly in this context – see however Monsen et al. (2002) –. The application of the raw tidal prism method provides an estimate of the mean residence time for the estuary while the introduction of the return coefficient, *i.e.* the fraction of water leaving during ebb that returns during flood, corresponds to the concept of exposure time (e.g. Dyer, 1991; Sanford et al., 1992; Cucco and Umgiesser, 2006).

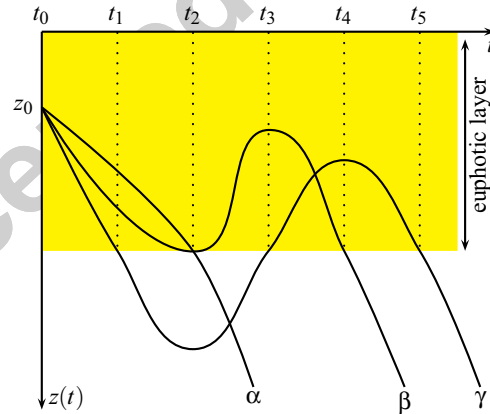


Figure 3: Hypothetic paths of three particles released at time t_0 at the same depth z_0 in the euphotic layer (More realistic paths can be seen in Spivakovskaya et al. (2007)). Both particles labeled α and β have the same residence time $t_2 - t_0$. The residence time of the particle labeled γ is $t_1 - t_0$. The total times spent by the three particles α , β and γ in the euphotic layer, *i.e.* their exposure times, are respectively $t_2 - t_0$, $t_4 - t_0$ and $(t_1 - t_0) + (t_5 - t_3)$.

Mathematically, the (mean) exposure time at a depth z_0 and a time t_0 is given by (Delhez, 2006)

$$\Theta(t_0, z_0) = \int_{t_0}^{\infty} \int_0^h C(t, z) dz dt \quad (8)$$

where $C(t, z)$ is the concentration field induced by a unit point discharge at $z = z_0$ at time $t = t_0$. In the 1D vertical

model considered here, this is the solution of the initial value problem

$$\frac{\partial C}{\partial t} + \frac{\partial}{\partial z}(wC) = \frac{\partial}{\partial z} \left(\lambda \frac{\partial C}{\partial z} \right) \quad (9)$$

$$C(t_0, z) = \delta(z - z_0) \quad (10)$$

where $\delta(z - z_0)$ is the Dirac generalized function modeling a point release at $z = z_0$. The model accounts for spatial and temporal variations of both w and λ . In the following, we will assume, like in the previous section, that the settling velocity and the diffusivity coefficient do not vary with time. In this case, the exposure time is a function of the only vertical coordinate.

Contrary to the computation procedure for the residence time (Delhez et al., 2004), the initial value problem (9)-(10) must be solved not only in the control domain in which the exposure time is sought, *i.e.* the euphotic layer in the context of the current study, but also in the larger domain where the tracer can be transported, *i.e.* in the whole water column. One must indeed be able to describe explicitly the processes that can bring back the particles in the euphotic layer. (A similar requirement is stressed by Sanford et al. (1992) in the context of the tidal flushing of estuaries : the return coefficient in an estuary can only be computed by taking into account the flow field outside that estuary.) The boundary conditions of the differential problem (9)-(10) must therefore be applied at the surface and at the bottom of the water column. Assuming that the flux of particles through the surface is zero and that the particles can settle on the bottom (where H is the total depth of the water column), one has

$$-w(z)C + \lambda(z) \frac{\partial C}{\partial z} \Big|_{z=0} = 0 \quad (11)$$

$$\lambda(z) \frac{\partial C}{\partial z} \Big|_{z=H} = 0 \quad (12)$$

The introduction of a Dirac generalized function as the initial condition (10) of the above differential problem can be seen at first sight as a mathematical trick that has nothing to do with the real world. It is however the appropriate mathematical way to describe the path and fate of hypothetical particles or phytoplankton cells like those displayed in Fig. 3 but with the usual Eulerian approach underlying the advection-diffusion equation (9). In the same way as particles/phytoplankton cells initially released at the same depth will follow different paths, the initial point source (10) will evolve into a cloud spreading vertically because of diffusion as it settles down at the sinking velocity w .

The solution of (9)-(12) is also the elementary building block with which one can reconstruct the fate of the particles forming an arbitrary initial continuous vertical profile. Denoting temporarily the solution of the differential problem (9)-(12) for a given z_0 as $\mathcal{G}(t, z; z_0) = C(t, z)$, the evolution of the vertical profile $\tilde{C}_0(z)$ can be shown to be given by

$$\tilde{C}(t, z) = \int_0^H \tilde{C}_0(z_0) \mathcal{G}(t, z; z_0) dz_0 \quad (13)$$

i.e. $\mathcal{G}(t, z; z_0)$ is the Green function of the advection/diffusion problem (e.g. Morse and Feshbach, 1999). Although derived from an apparently unrealistic point source, the Green function contains in it much more information (all of it, actually) about the dynamics than the time evolution of a realistic vertical profile. The gradients in a particular vertical profile of phytoplankton concentration can be related to the net vertical transport by turbulent diffusion. This net transport is however the algebraic difference between two raw turbulent fluxes directed in opposite directions and controlling the entrainment of individual particles or phytoplankton cells into deeper or shallower layers. In the particular case of an homogeneous vertical profile, there is no net vertical transport by diffusion but the individual particles undergo compensating vertical turbulent movements that are described by the solution of (9)-(12). These equation are therefore used in this study since we aim at the description of the vertical movement of the individual particles / phytoplankton cells.

The advection-diffusion equation (9) is obviously appropriate to compute the exposure time of inert particles that, with the exception of their settling velocity, have no proper dynamics and are simply transported by the mean flow and by turbulence. The equation (9) does not contain any term related, for instance, to the growth rate of phytoplankton and, therefore, cannot be used to describe the dynamics of a phytoplankton population. Obviously, the dynamics of the whole population and, for instance, the occurrence of deep water maximum of chlorophyll depend on a balance

between sedimentation, turbulent diffusion and growth (e.g. Huisman and Sommeijer, 2002; Huisman et al., 2002; Wong et al., 2007). The aim of this study is however to follow individual phytoplankton cells and diagnose the influence of turbulence on the time that each of them spent in the euphotic layer once it appears in the water column. In this context and in line with previous studies (e.g. Lande and Wood, 1987; Ruiz, 1996; Franks, 2001; Deleersnijder et al., 2006a; Ross, 2006) the growth rate is not included in the equation (9). The light conditions encountered by the cells during their vertical movements and their influence on the growth rate are however considered in section 5.

As an alternative to solving (8)-(12), and in a much more efficient way, the mean exposure time in the euphotic layer can be computed using the adjoint method introduced by Delhez et al. (2004) for the residence time. In the particular context of the 1D vertical model used here, with both w and λ constant in time, one has

$$w(z)\frac{d\Theta}{dz} + \frac{d}{dz}\left(\lambda(z)\frac{d\Theta}{dz}\right) + \delta_{]0,\ell[}(z) = 0 \quad (14)$$

$$\lambda(z)\frac{d\Theta}{dz}\Big|_{z=0} = 0 \quad (15)$$

$$w(z)\Theta + \lambda(z)\frac{\partial\Theta}{\partial z}\Big|_{z=H} = 0 \quad (16)$$

where $\delta_{]0,\ell[}$ is the characteristic function of the euphotic layer, *i.e.*

$$\delta_{]0,\ell[}(z) = \begin{cases} 1 & \text{for } z \in]0,\ell[\\ 0 & \text{elsewhere} \end{cases} \quad (17)$$

Equation (14) is identical to (5) in the euphotic layer. In the thermocline, its source term $\delta_{]0,\ell[}$ vanishes. This accounts for the fact that the time spent by the particles below the euphotic layer does not contribute to the exposure time.

The whole mathematical procedure leading to the adjoint model is presented in appendix B.

The differential problem (14)-(16) can be used to compute the exposure time for any vertical profile of the settling velocity w and the diffusion coefficient λ . A general analytical solution can be derived and is given in appendix C.

The vertical profiles of the exposure time for the two-layer model considered in Fig. 2 are plotted in Fig. 4.

The main difference between Fig. 4 and the corresponding figure for the residence time is the behavior of these two diagnostics at the bottom of the euphotic layer. While the residence time vanishes at $z = \ell$, the exposure time differs from zero. This non zero value of the exposure time reflects the probability that a particle reaching the bottom of the euphotic layer moves upward immediately or at a later time. This probability is itself a function of the strength of the vertical mixing. When the diffusion coefficient is very small in the thermocline (reference solid curve and dashed curves in Fig. 4), this probability is low, $\Theta(\ell)$ is close to zero, and the exposure time is near equal to the residence time. When λ_b increases, while still much smaller than λ_s , the probability for a particle reaching the depth $z = \ell$ to move back in the euphotic layer through vertical mixing becomes significant and the exposure time differs from zero at the bottom of the euphotic layer. This probable return has a clear impact on the exposure time not only in the thermocline but also in the surface mixed layer where the exposure time is then much larger than the residence time.

Just like the residence time in Fig. 2, the exposure time in Fig. 4 increases in the surface mixed layer when λ_s increases. While the value taken by the residence time in the surface mixed layer is rather sensitive to λ_b , the diffusion coefficient in the thermocline has little influence on the exposure time. In the thermocline, the exposure time increases with λ_b while the residence times shows a non monotonic dependency. For all the combinations of parameters considered in Fig. 4, the exposure time is larger than the advection time scale. All together, in the simplified model considered here, an increase of the diffusion coefficient at any depth helps phytoplankton cells to spend a longer total time in the euphotic layer, irrespective of their initial depth.

The conceptual difference between the residence time and the exposure time is the fact that the former measures the time needed for a particle to hit the bottom of the euphotic layer for the first time while the latter measures the time spent in the euphotic layer until the particle has definitely left the euphotic layer. It is therefore not surprising that the larger differences between the two figures 2 and 4 occur when the diffusion coefficient in the thermocline increases for the thermocline acts then as a less severe barrier inhibiting vertical exchanges and the probabilities of

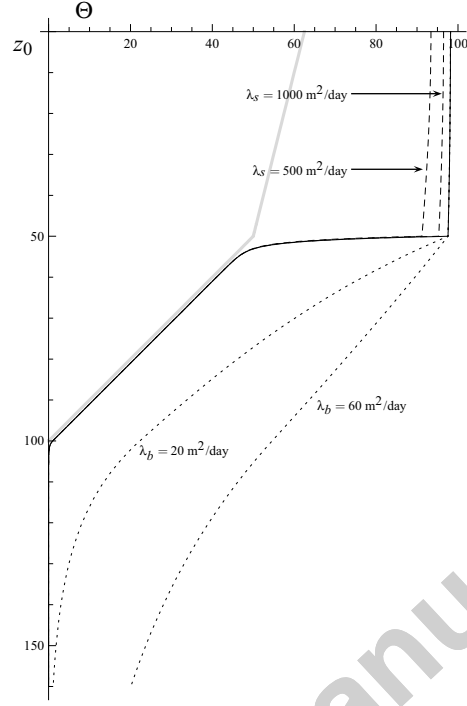


Figure 4: Vertical profiles of the exposure time (in days) in the euphotic layer for the two-layer model considered in Fig. 2 with $m = 50$ m, $\ell = 100$ m, $w_s = 4$ m/day, $w_b = 1$ m/day. The total depth of the water column H is 500 m. The solid curve is obtained with $\lambda_s = 2000$ m²/day and $\lambda_b = 1$ m²/day. Taking this curve as a reference and decreasing the diffusion coefficient in the surface layer to $\lambda_s = 1000$ m²/day and $\lambda_s = 500$ m²/day (dashed curves) has little effect in the thermocline and slightly decreases the exposure time of particles initially located in the surface mixed layer. Using the same solid curve as a reference but increasing λ_b to 20 m²/day and 60 m²/day (dotted curves) has no influence in the surface mixed layer but strongly increases the exposure time of particles initially located in the thermocline.

exchanges between the surface mixed layer and the thermocline increases. Particles initially located in the surface mixed layer have then a higher probability to leave this layer and the euphotic layer within a given period of time so that their residence time decreases. For the exposure time, the effect of a higher diffusion coefficient is compensated by the corresponding higher probability for particles below the surface mixed layer or the euphotic layer to move up.

So far we assumed the euphotic layer to be deeper than the surface mixed layer so that the bottom of the euphotic layer is in the thermocline. Consider however for a while the opposite situation where the euphotic layer is shallower than the surface mixed layer. In this case, the diffusion coefficient at the bottom of the euphotic layer is large and significant differences between the residence time and the exposure time in the euphotic layer can be expected. Fig. 5 shows for instance the residence time and the exposure time in a 30 meter deep euphotic layer when the depth of the surface mixed layer is 50 meters. In this case, the residence time takes a very small value that reflects the very efficient vertical mixing : in Fig. 5, any particle initially in the euphotic layer leaves this layer and reaches the bottom of the surface mixed layer in less than half a day. The exposure time is much larger because the particles are mixed throughout the whole surface layer and are repeatedly, but in an intermittent way, present in the euphotic layer. Although the exposure time measures only the time spent in the top 30 meters, it is nearly constant over the whole surface mixed layer. All the particles in the surface mixed layer have indeed similar paths and histories. Clearly, the concept of residence time is inappropriate to diagnose the presence of phytoplankton cell in the euphotic layer. The exposure time behaves as expected and reflects both the vertical structure of the water column and the influence of vertical mixing on the light conditions encountered by the phytoplankton cells. Because the latter spent a significant part of their time below the euphotic layer, the exposure time shown in Fig. 5 is much smaller than in Fig. 4.

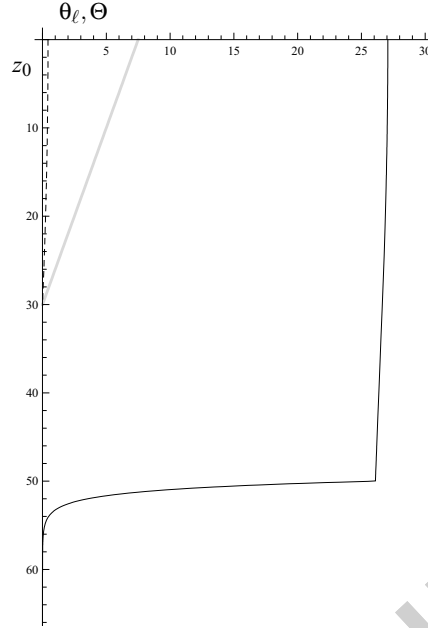


Figure 5: Vertical profiles of the residence time (in days, dashed line) and exposure time (in days, solid line) in the euphotic layer for the two-layer model considered in Fig. 2 with $\lambda_s = 1000 \text{ m}^2/\text{day}$, $\lambda_b = 1 \text{ m}^2/\text{day}$, $w_s = 4 \text{ m/day}$, $w_b = 1 \text{ m/day}$. The euphotic layer is assumed to be shallower than the surface mixed layer, *i.e.* $\ell = 30 \text{ m}$ and $m = 50 \text{ m}$. The total depth of the water column H is 500 m . The advection time scale is plotted for reference with a thick gray line.

4. Effect of diffusion on the residence time and the exposure time.

The simplified two-layer model considered above, with piecewise constant profiles of the settling velocity and diffusion coefficient, provides only a first glimpse of the effect of turbulent diffusion on the residence time and the exposure time in the euphotic layer. The reality is however more complex, even in the restricted context of a 1D steady-state model.

Consider first the case when the vertical settling velocity is constant over the whole water column. Then, the exposure time can be expressed as (see appendix C)

$$\Theta(z) = \frac{\ell - z}{w} + \frac{1}{w} \int_0^z \exp \left[-w \int_\xi^z \frac{du}{\lambda(u)} \right] d\xi \quad z < \ell \quad (18)$$

in the euphotic layer and

$$\Theta(z) = \frac{1}{w} \int_0^\ell \exp \left[-w \int_\xi^z \frac{du}{\lambda(u)} \right] d\xi \quad z \geq \ell \quad (19)$$

in the thermocline. The first term in the right-hand-side of (18) is the advection time scale, *i.e.* the residence/exposure time in the euphotic layer when diffusion is neglected. Since the integral in (18) is positive, the exposure time is always larger than the advection time scale.

A careful look at (18) shows that the exposure time at a given depth depends only on the diffusivity coefficient at shallower depths and that it is a monotonically increasing function of the turbulent diffusion coefficient. Therefore, any increase of the diffusion coefficient around a given depth z induces an increase of the exposure time at all depths below z .

No such general conclusions can be drawn for the residence time (unless the diffusion coefficient vanishes in the thermocline, see Deleersnijder et al. (2006b)).

These general conclusions about the exposure time are valid for any vertical distribution $\lambda(z)$ of the diffusion coefficient. Consider for instance the problem addressed by Ross (2006) who computed the residence time in the surface mixed layer with the diffusion coefficient

$$\lambda(z) = \begin{cases} \lambda_{bg} + \frac{\lambda_{max}}{2} \left(1 - \cos \frac{2\pi z}{m} \right) & z \leq m \\ \lambda_{bg} & z > m \end{cases} \quad (20)$$

In this expression λ_{bg} is a small background diffusivity and λ_{max} is the maximum diffusivity coefficient at mid depth of the surface mixed layer. The residence time and the exposure time in the surface mixed layer (*i.e.* assuming that $m = \ell$) computed for various values of the parameters are plotted in Fig. 6. Our results for the residence time are in sharp contrast with those shown by Ross (2006) (This author do not provide vertical profiles of the residence time but computed the residence time only at a single depth with a numerical random walk model). The vertical profiles of the residence time do not support the claim that turbulence helps phytoplankton cells to remain in suspension in the surface mixed layer. The residence time can indeed be much smaller than the advection time scale. The exposure time in the surface mixed layer provides however the required arguments : the total time spent by phytoplankton cells in the surface mixed layer increases monotonically at all depths with the intensity of turbulent mixing. The exposure time is also much less sensitive to the background diffusivity than the residence time.

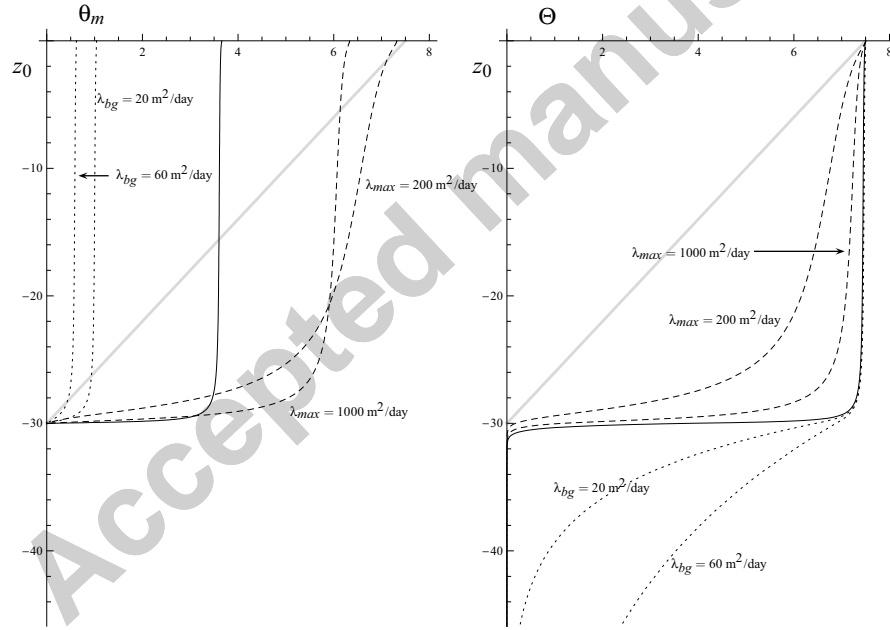


Figure 6: Vertical profiles of the residence time (right) and exposure time (left), in days, in a 30 m deep surface mixed layer using the diffusivity profile (20). The reference solid curve is computed with $w = 4$ m/day, $\lambda_{max} = 8000$ m²/day and $\lambda_{bg} = 1$ m²/day. The total depth of the water column H is 500 m. The tick gray curve is the advection time-scale. Decreasing the diffusion coefficient in the surface layer to $\lambda_{max} = 1000$ m²/day and $\lambda_{max} = 200$ m²/day (dashed curves) reduces the exposure time at all depths in the surface mixed layer but has a variable effect on the residence time. The residence time exhibits a large sensitivity to the background diffusivity (dotted curves for $\lambda_{bg} = 20$ m²/day and $\lambda_{bg} = 60$ m²/day) while this has no influence on the exposure time for particles initially located in the surface mixed layer.

Although the settling velocity is not a constant in Fig. 4 (only piecewise constant), the exposure time exhibits the same properties as in the case of a constant settling velocity : it is monotonically increasing function of the diffusion coefficient, is always larger than the advection time scale and its value in the surface mixed layer is rather insensitive to the diffusion coefficient in the thermocline. Using the analytical expression (C-9) of the exposure time derived in the appendix, the two first properties can indeed be generalized to depth-variant settling velocity and diffusion coefficient provided $w(z)$ is a non-increasing function of depth. In this case, the exposure time increases with the

diffusion coefficient so that turbulence does help sinking phytoplankton cells to spend a longer time in the euphotic layer. When the settling velocity is a function of the vertical coordinate, the background diffusion coefficient, or, more generally, the turbulence conditions below the mixed layer and/or the euphotic layer can however influence the exposure time in the surface layer.

When the settling velocity increases with depth, turbulence can influence the exposure time in both ways. Consider for instance the same configuration as in Fig. 6 but assume this time that the settling velocity increases with depth from $w_s = 4$ m/s in the surface mixed layer to $w_b = 8$ m/s below the euphotic layer according to

$$w(z) = \begin{cases} w_s & z < m \\ w_s + (w_b - w_s) \frac{z - m}{z - \ell} & m \leq z < \ell \\ w_b & z \geq \ell \end{cases} \quad (21)$$

The settling velocity is usually a function of the density difference between the particle and the surrounding water and should therefore be a decreasing function of depth in a stable water column. An increase of the settling velocity can however be due aggregation/flocculation processes that increase the effective size of the sinking particles/flocs. The residence time in the surface mixed layer is not affected since the settling velocity is not modified in that layer. The vertical profiles of the exposure time in the surface mixed layer using the profile (21) and the diffusion coefficient (20) are shown in Fig. 7. Now, the exposure time is not larger than the advection time and depend also in a non monotonic way on the diffusion coefficient. The neat properties highlighted in the case of a constant settling velocity cannot be extended to the general case when the settling velocity varies with depth. The exposure time remains a very valuable diagnostics to quantify the total time spent by particles or phytoplankton cells in the surface mixed layer or the euphotic layer but, unless the settling velocity can be considered as a constant or decreases with depth, the effect of turbulence must be studied case by case.

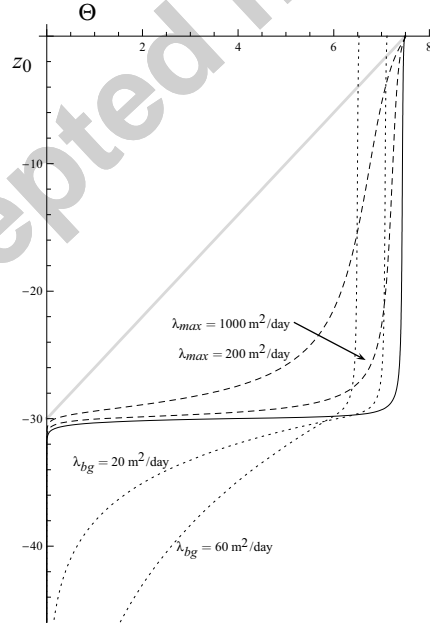


Figure 7: Vertical profiles of the exposure time (in days), in a 30 m deep surface mixed layer using the diffusivity profile (20) and a settling velocity increasing from $w_s = 4$ m/day in the surface mixed layer to $w_b = 8$ m/day at 100 m depth according to (21). The reference solid curve is computed with $\lambda_{max} = 8000$ m²/day and $\lambda_{bg} = 1$ m²/day. The total depth of the water column H is 500 m. The tick gray curve is the advection time-scale. The dashed curves are obtained by decreasing λ_{max} to 1000 m²/day and 200 m²/day. The dotted curves correspond to variations of the background diffusion coefficient. The exposure time can be smaller than the advection time and depends in a non monotonic way on the diffusion coefficient.

5. Light exposure.

The light intensity to which phytoplankton cells are exposed in the euphotic layer varies with depth. For instance, assuming that the light extinction coefficient takes a constant value α , the light intensity $I(z)$ is given by the well-known Beer-Lambert law

$$I(z) = I_0 e^{-\alpha z} \quad (22)$$

where I_0 is the light intensity at the surface. The important factor for the development of phytoplankton cells is therefore not only the time spent in the euphotic layer, *i.e.* their exposure time, but also the actual level of irradiance that they receive.

In practice, the depth of the euphotic layer is also not clearly defined. While the value $1/\alpha$ can then be taken as an order of magnitude of the depth of the euphotic layer, it does not define a clear bottom boundary for the euphotic layer.

In order to take these aspects into account, we introduce a weighted average version of the exposure time where the time spent at a given depth is weighted by the light intensity at this level. From the concentration field produced by the release of phytoplankton cells at a given depth z_0 as in (9)-(10), we define the *light exposure* as

$$\Theta_I(z_0) = \int_0^\infty \int_0^H C(t, z) I(z) dz dt \quad (23)$$

This diagnoses the total amount of light energy (per horizontal area unit) to which the phytoplankton cells are exposed during their cycling through the water column.

A further generalization of the exposure time can be introduced to take into account the fact that the growth rate of phytoplankton is a function $f(I)$ of light intensity. The functional forms commonly used to model the phytoplankton response to irradiance range from a simple linear response to incident light, to a non-linear response taking into account photo-inhibition, and include various non-linear saturating responses (e.g. Franks, 2002; Fennel and Neumann, 2004). Using the phytoplankton response $f[I(z)]$ to weight the time spent at a given depth leads to the *effective light exposure*

$$\Theta_f(z_0) = \int_0^\infty \int_0^H C(t, z) f[I(z)] dz dt \quad (24)$$

Both the light exposure and the effective light exposure generalize the concept of exposure time. They are also easily integrated in the mathematical framework developed for the residence and exposure times. The corresponding adjoint steady-state model for the effective light exposure, for instance, is given by (See appendix B.)

$$w(z) \frac{d\Theta_f}{dz} + \frac{d}{dz} \left(\lambda(z) \frac{d\Theta_f}{dz} \right) + f[I(z)] = 0 \quad (25)$$

$$\lambda(z) \frac{d\Theta_f}{dz} \Big|_{z=0} = 0 \quad (26)$$

$$w(z) \Theta_f + \lambda(z) \frac{\partial \Theta_f}{\partial z} \Big|_{z=H} = 0 \quad (27)$$

where it is assumed, as in the previous section, that the phytoplankton cells can settle on the bottom and are never resuspended in the water column. An analytical solution of (25)-(27) for arbitrary spatial variations of w , λ , I , and any functional form f is derived in the appendix C.

In the particular case of a constant sinking velocity w , the effective light exposure can be expressed as

$$\Theta_f(z) = \frac{1}{w} \int_z^H f[I(\xi)] d\xi + \frac{1}{w} \int_0^z f[I(\xi)] \exp \left[-w \int_\xi^z \frac{du}{\lambda(u)} \right] d\xi \quad (28)$$

The light exposure can be put in a similar form.

When turbulence is weak, the second term in (28) is negligible and the effective light exposure reduces to the first term that measures the functional response of phytoplankton cells sinking through the water column at the constant velocity w . When diffusion is added to the system, turbulence increases the exposure time of the sinking phytoplankton

cells, the total amount of light energy that they receive and their effective light exposure. Using the general solution (C-9) derived in appendix C, the conclusions can be extended to the case when the settling velocity does not increase with depth.

It must be noted that the results demonstrate the effect of the only hydrodynamics processes on the fate of phytoplankton cells. While the physiological response, including photo-inhibition, can be taken into account through the functional form f , the complex dynamics of photoadaptation (e.g Lewis et al., 1984; Dusenberry et al., 2001) is ignored : phytoplankton cells are assumed to adapt immediately to the light conditions.

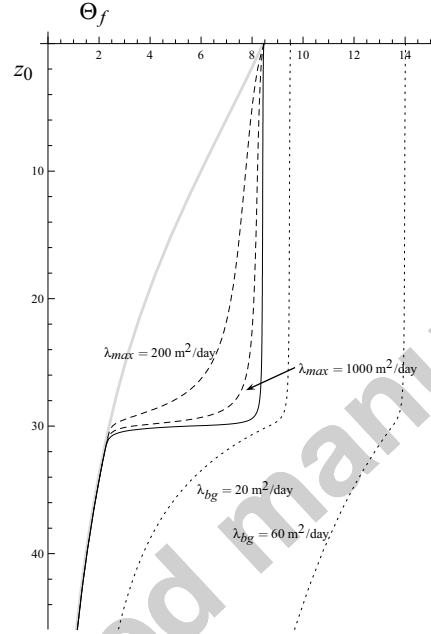


Figure 8: Vertical profiles of the effective light exposure (in days) using (20), (21), (22) and (29) with $m = 30$ m, $I_0 = 1.5I_{opt}$, $\alpha = 2/m$, $w_s = 4$ m/day, $w_b = 1$ m/day, $\ell = 100$ m and $H = 500$ m. The reference solid curve is computed with $\lambda_{max} = 8000$ m²/day and $\lambda_{bg} = 1$ m²/day. The tick gray curve is the effective light exposure when diffusion is neglected. The dashed curves are obtained by decreasing λ_{max} to 1000 m²/day and 200 m²/day. The dotted curves correspond to variations of the background diffusion coefficient.

As an example, figure 8 shows the effective light exposure of phytoplankton cells when photo-inhibition is taken into account through the functional form

$$f(I) = \frac{I}{I_{opt}} \exp\left(1 - \frac{I}{I_{opt}}\right) \quad (29)$$

(Steele, 1962) where I_{opt} is the optimal light intensity. The light conditions are assumed to be described by (22) with $I_0 = 1.5I_{opt}$ and $\alpha = 2/m$ where $m = 30$ m is the depth of the surface mixed layer. The turbulent diffusivity coefficient is given by (20) and the settling velocity varies according to (21) between $w_s = 4$ m/day in the surface mixed layer to $w_b = 1$ m/day at a depth $\ell = 100$ m. Because of the strong mixing, all the particles in the surface mixed have nearly the same effective light exposure since they cycle repeatedly through the whole surface mixed layer, whatever their initial depth. The effective light exposure appears as an increasing function of both the maximum and the background diffusion coefficients. Turbulence helps phytoplankton cells to receive more light energy and favors their development. When the background diffusivity is small and vertical mixing is strongly inhibited between the surface mixed layer and the thermocline, the effective light exposure at the surface is very close to the value that it would take if diffusion was neglected. This puzzling behavior was already mentioned by Deleersnijder et al. (2006a) for the residence time when the diffusion coefficient vanishes in the thermocline. In a well defined two layer structure of the water column where turbulence is high in the surface mixed layer and the background diffusivity coefficient is vanishingly small,

the effective light exposure can therefore be estimated from the corresponding profile

$$\Theta_f^\infty(z_0) = \int_{z_0}^H \frac{f[I(z)]}{w(z)} dz \quad (30)$$

when diffusion is ignored : Θ_f approximately takes the constant $\Theta_f^\infty(0)$ in the surface mixed layer and is close to Θ_f^∞ in the thermocline. The effective light exposure in figure 8 shows however a large sensitivity to the value of the background diffusion coefficient. When turbulent fluctuations are not completely inhibited in the thermocline, the effective light exposure at the surface can be larger than $\Theta_f^\infty(0)$. A careful analysis of the influence of the parameters considered to produce Fig. 8 reveals that these larger values of Θ_f are favored by the decrease of the settling velocity in the thermocline. Because of this reduced settling velocity, particles tend to accumulate below the surface mixed layer and have therefore a larger probability to be sucked by diffusion in the surface mixed layer if the background diffusion coefficient is not too small.

6. Conclusion.

Different diagnostic tools can be used to quantify the time spent by particles in the surface layer and the influence of diffusion on the survival of settling phytoplankton cells.

While by far the most widely used diagnostic variable, the residence time in the euphotic layer suffers from an inappropriate treatment of the particles at the bottom of the euphotic layer. The common approach according to which the particles are discarded from the computation of the residence time as soon as they reach for the first time the bottom of the euphotic layer can lead to the underestimation of the total time spent by these particles in the euphotic layer. This is particular true when the diffusion coefficient at the bottom of the euphotic layer is large, *e.g.* when the euphotic layer is shallower than the surface mixed layer.

The exposure time is a more appropriate diagnostic variable because it takes into account the possibility that particles having left the euphotic layer can re-enter this layer at a later time. The results obtained in the particular context of a 1D vertical model with constant hydrodynamic conditions show that, contrary to the residence time, the exposure time in the euphotic layer increases monotonically with the intensity of turbulence, at least when the settling velocity does not increase with depth. Increasing the diffusion coefficient allows settling particles to spend a longer time in the euphotic layer.

The concept of exposure time can be generalized to capture more of the dynamics of phytoplankton cells settling through the euphotic layer. Weighting the time spent by phytoplankton cells at each level by the prevailing light intensity leads to the definition of the light exposure, which measures the total light energy received by the cells during their cycling in the water column. Using the functional response to the light intensity at a given depth as a weight factor leads to the new concept of effective light exposure.

Technically, the light exposure and the effective light exposure can be computed using natural extensions of both the direct and adjoint approaches introduced previously for the residence and exposure time (Delhez et al., 2004). In particular, a differential equation has been derived in the context of a 1D vertical model and an analytical solution is also given.

When the settling velocity does not increase with depth, the light exposure and effective light exposure at a given depth z appears as monotonically increasing functions of the diffusion coefficient. Therefore, turbulence definitely helps sinking phytoplankton species to survive, for it increases the amount of light their cells are exposed to.

In the less frequent situation when the settling velocity increases with depth, no general conclusion can be given. The concepts of exposure time, light exposure and effective light exposure continue to be very valuable diagnostics to quantify the effect of turbulence on the light conditions undergone by sinking phytoplankton cells but the effect of turbulence must be studied case by case.

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Appendix.

A. Singular behavior of the residence time.

The singular behavior of the residence time when the diffusion coefficient tends to zero and the possibility for the residence time to take a non zero value at the bottom of the control domain in which it is computed can be illustrated by resorting to the solution (1)-(3) of the two-layer model given by Lande and Wood (1987).

The only requirement for (1)-(3) to be valid is that the settling velocities w_s and w_b are not zero. The solution can therefore be used to compute the residence time in the particular case when the euphotic layer corresponds exactly with the surface mixed layer.

When $\lambda_b \neq 0$ and for the points in the surface mixed layer ($z < m$), one computes

$$\lim_{\ell \rightarrow m} \theta_\ell(z) = \lim_{\ell \rightarrow m} [\theta_m(z) + \theta_\ell(m)] = \theta_m(z) \quad (\text{A-1})$$

since

$$\lim_{\ell \rightarrow m} \theta_\ell(m) = 0 \quad (\text{A-2})$$

Because $\theta_m(z)$ does not depend on the diffusion coefficient λ_b in the thermocline, the residence time in the euphotic layer is also given by

$$\frac{m-z}{w_s} - \frac{\lambda_s}{w_s^2} \left(e^{-zw_s/\lambda_s} - e^{-mw_s/\lambda_s} \right) \quad (\text{A-3})$$

in the limit case when the diffusion coefficient vanishes in the thermocline.

Consider now the general two-layer model leading to (1)-(3) and assume first that λ_b is zero. One gets,

$$\lim_{\lambda_b \rightarrow 0} \theta_\ell(m) = \frac{\ell-m}{w_b} + \frac{\lambda_s}{w_1 w_2} \left(1 - e^{-mw_s/\lambda_s} \right) \quad (\text{A-4})$$

The additional assumption that the euphotic layer coincides with the surface mixed layer, *i.e.* $m = \ell$, leads then to a residence time given by

$$\frac{m-z}{w_s} - \frac{\lambda_s}{w_s^2} \left(e^{-zw_s/\lambda_s} - e^{-mw_s/\lambda_s} \right) + \frac{\lambda_s}{w_1 w_2} \left(1 - e^{-mw_s/\lambda_s} \right) \quad (\text{A-5})$$

that differs from (A-4) and takes a non zero value at the bottom of the euphotic layer, as discussed by Deleersnijder et al. (2006b). In other words, one has

$$\lim_{\ell \rightarrow m} \left[\lim_{\lambda_b \rightarrow 0} \theta_\ell(z) \right] \neq \lim_{\lambda_b \rightarrow 0} \left[\lim_{\ell \rightarrow m} \theta_\ell(z) \right] \quad (\text{A-6})$$

This singular behavior of the residence time partly explains the conflicting results obtained by various authors. Both behaviors (A-4) and (A-5) were computed by Spivakovskaya et al. (2007) using a single model set-up but with, respectively, an forward Itô random walk and a backward Itô random walk model.

B. Adjoint model for a generalized exposure time.

In the general framework of an unsteady model of the water column, the generalized exposure in the euphotic layer defined by

$$\Theta_g(t_0, z_0) = \int_0^H dz \int_{t_0}^{\infty} C(t, z) g(t, z) dt \quad (\text{B-1})$$

can be computed for an arbitrary weight function g from the concentration field $C(t, z)$ produced by a unit point discharge at time t_0 at the depth $z = z_0$. Assuming a no flux condition at the surface and allowing for the settling of particles on the bottom, this concentration field is the solution of the differential problem (9)-(12).

Setting

$$g(t, z) = \delta_{[0, \ell]}(z) \quad (\text{B-2})$$

in (B-1) leads to the exposure time. The light exposure and the effective light exposure correspond respectively to

$$g(t, z) = I(t, z) \quad (\text{B-3})$$

where I is the light intensity and

$$g(t, z) = f(I(t, z)) \quad (\text{B-4})$$

where $f(I)$ is the response curve.

A differential problem like (9)-(12) must be solved for each initial depth z_0 and, possibly, for each initial time t_0 , where and when the generalized exposure is sought. The determination of the vertical profile of the generalized exposure requires therefore repeated computations for different initial conditions. Such a set of unsteady differential problems must be solved even if the hydrodynamic conditions and the light conditions are in a steady state and the weight function f does not depend on t_0 .

As an alternative to the direct approach described above, the adjoint approach introduced by Delhez et al. (2004) for the residence time can be adapted as follows.

For an arbitrary time T , we define

$$C_g(T; t_0, z_0) = \int_0^H C(T, z) g(T, z) dz \quad (\text{B-5})$$

which can be seen as the contribution of time T to the generalized exposure Θ_g . Introducing then the adjoint variables $C_{T,g}^*(t, z)$ in

$$C_g(T; t_0, z_0) = \int_0^H C(T, z) g(T, z) dz - \int_{t_0}^T dt \int_0^H C_{T,g}^* \left\{ \frac{\partial C}{\partial t} + w \frac{\partial C}{\partial z} - \frac{\partial}{\partial z} \left(\lambda \frac{\partial C}{\partial z} \right) \right\} dz \quad (\text{B-6})$$

and, following the same reasoning as in Delhez et al. (2004), one obtains

$$C_g(T; t_0, z_0) = C_{T,g}^*(t_0, z_0) \quad (\text{B-7})$$

if $C_{T,g}^*$ is the solution of

$$\begin{cases} \frac{\partial C_{T,g}^*}{\partial t} + w \frac{\partial C_{T,g}^*}{\partial z} + \frac{\partial}{\partial z} \left(\lambda \frac{\partial C_{T,g}^*}{\partial z} \right) = 0 \\ C_{T,g}^*(T, z) = g(T, z) \end{cases} \quad (\text{B-8})$$

with the adjoint boundary conditions

$$\begin{cases} \lambda \frac{\partial C_{T,g}^*}{\partial z} \Big|_{z=0} = 0 \\ w C_{T,g}^* + \lambda \frac{\partial C_{T,g}^*}{\partial z} \Big|_{z=H} = 0 \end{cases} \quad (\text{B-9})$$

The distribution of the generalized exposure of the particles forming the initial patch can be described by

$$D_g(t_0, \tau, z_0) = C_g(t_0 + \tau; t_0, z_0) = C_{t_0+\tau,g}^*(t_0, z_0) \quad (\text{B-10})$$

which is a cumulative distribution function of the generalized exposure. It is the solution of

$$\begin{cases} \frac{\partial D_g}{\partial t} - \frac{\partial D_g}{\partial \tau} + w \frac{\partial D_g}{\partial z} + \frac{\partial}{\partial z} \left(\lambda \frac{\partial D_g}{\partial z} \right) = 0 \\ D_g(t, 0, z) = g(t, z) \end{cases} \quad (\text{B-11})$$

This expression generalizes the differential equation introduced by Delhez et al. (2004) for the cumulative distribution function of the residence time.

Since the mean is the zero-th order moment of the cumulative distribution function, *i.e.*

$$\Theta_g(t_0, z_0) = \int_0^\infty D_g(t_0, \tau, z_0) d\tau \quad (\text{B-12})$$

the mean generalized exposure satisfies the differential equation

$$\frac{\partial \Theta_g}{\partial t} + g(t, z) + w \frac{\partial \Theta_g}{\partial z} + \frac{\partial}{\partial z} \left(\lambda \frac{\partial \Theta_g}{\partial z} \right) = 0 \quad (\text{B-13})$$

that can be obtained by integrating (B-11) with respect to τ . The corresponding boundary conditions

$$\lambda \frac{\partial \Theta_g}{\partial z} \Big|_{z=0} = 0 \quad (\text{B-14})$$

$$w \Theta_g + \lambda \frac{\partial \Theta_g}{\partial z} \Big|_{z=H} = 0 \quad (\text{B-15})$$

are obtained from (B-9) in a similar way.

Equation (B-13) is an ordinary advection-diffusion equation similar to the advection-diffusion equation used in the direct approach. There are however two differences. First, the equation for the generalized exposure includes the additional source term $g(z, t)$. Second, in the unsteady case, the equation must be integrated backward in time and with the reversed flow, *i.e.* with w changed to $-w$.

The method is easily extended to more general model configurations. In a 3D model, the differential equation for the generalized exposure can be written as

$$\frac{\partial \Theta_g}{\partial t} + g(t, z) + (\mathbf{v} + \mathbf{w}) \cdot \nabla \Theta_g + \nabla \cdot [\mathbf{K} \cdot \nabla \Theta_g] = 0 \quad (\text{B-16})$$

where \mathbf{v} is the velocity vector, \mathbf{w} is the sinking velocity and \mathbf{K} is the diffusion tensor.

C. Steady state solution of the generalized exposure 1D equation.

The steady state version of the differential problem (B-13)-(B-15) for the generalized exposure can be solved for arbitrary spatial distributions of the sinking velocity $w(z)$, diffusivity coefficient $\lambda(z)$ and weight function $g(z)$.

The resolution makes use of the integrating factor (it is assumed that the ratio w/λ does not have non integrable singularities, which is always the case when λ differs from zero everywhere)

$$\varphi(z) = \exp \left[\int_0^z \frac{w(\xi)}{\lambda(\xi)} d\xi \right] \quad (C-1)$$

such that

$$\varphi'(z) = \frac{w(z)}{\lambda(z)} \varphi(z) \quad (C-2)$$

and

$$\varphi(0) = 1 \quad (C-3)$$

Dropping the time derivative in (B-13) and multiplying it by φ , one gets

$$\frac{d}{dz} \left[\lambda(z) \varphi(z) \frac{d\Theta_g}{dz}(z) \right] = -\varphi(z) g(z) \quad (C-4)$$

A first integration gives

$$\lambda(z) \varphi(z) \frac{d\Theta_g}{dz}(z) = - \int_0^z \varphi(\xi) g(\xi) d\xi \quad (C-5)$$

where the boundary condition (B-14) at the surface has been taken into account. A second integration leads to

$$\Theta_g(z) = C + \int_z^H \left[\frac{1}{\lambda(u) \varphi(u)} \int_0^u \varphi(\xi) g(\xi) d\xi \right] du \quad (C-6)$$

where C is an integration constant that corresponds to the value of generalized exposure at the bottom of the water column. Using the bottom boundary condition (B-15), one gets finally

$$\Theta_g(z) = \frac{1}{w(H) \varphi(H)} \int_0^H \varphi(\xi) g(\xi) d\xi + \int_z^H \left[\frac{1}{\lambda(u) \varphi(u)} \int_0^u \varphi(\xi) g(\xi) d\xi \right] du \quad (C-7)$$

This expression can be modified using the relation

$$\frac{1}{\lambda(u) \varphi(u)} = - \frac{d}{du} \left[\frac{1}{w(u) \varphi(u)} \right] - \frac{w'(u)}{\varphi(u) w^2(u)} \quad (C-8)$$

and by integrating by parts the second integral in (C-7). One gets

$$\begin{aligned} \Theta_g(z) = & \int_z^H \frac{g(u)}{w(u)} du + \frac{1}{w(z)} \int_0^z g(\xi) \exp \left[- \int_\xi^z \frac{w(u)}{\lambda(u)} du \right] d\xi \\ & - \int_z^H \frac{w'(u)}{w^2(u)} \int_z^u g(\xi) \exp \left[- \int_\xi^u \frac{w(\zeta)}{\lambda(\zeta)} d\zeta \right] d\xi du \end{aligned} \quad (C-9)$$

The first term in this expression is the generalized exposure for a particle sinking through the water column at the velocity w without turbulence. When $w'(u) \leq 0$ at all depths, *i.e.* when the second and third terms of the right-hand-side are both positive and increase with λ . The generalized exposure is therefore an increasing function of the diffusion coefficient. When $w(z)$ increases with depth, the actual behavior of the generalized exposure depends on the balance between the three terms in (C-9).

When w is a constant, (C-9) can be used to express the exposure time in the euphotic layer of depth ℓ as

$$\Theta(z) = \begin{cases} \frac{\ell - z}{w} + \frac{1}{w} \int_0^z \exp \left[-w \int_\xi^z \frac{du}{\lambda(u)} \right] d\xi & z < \ell \\ \frac{1}{w} \int_0^\ell \exp \left[-w \int_\xi^z \frac{du}{\lambda(u)} \right] d\xi & z \geq \ell \end{cases} \quad (C-10)$$

The mathematical developments above can be used to compute the exposure time, the light exposure and the effective light exposure with the weight functions (B-2)-(B-4). The residence time in the euphotic layer can also be computed by substituting ℓ for H in (C-6) and setting $g(z) = 1$ and $C = 0$, since the residence time is zero at the bottom of this layer. One gets

$$\theta_\ell(z) = \int_z^\ell \left[\frac{1}{\lambda(u)\phi(u)} \int_0^u \phi(\xi) d\xi \right] du \quad (\text{C-11})$$

or, when w is constant,

$$\theta_\ell(z) = \frac{\ell - z}{w} + \frac{1}{w} \int_0^z \exp \left[-w \int_\xi^z \frac{du}{\lambda(u)} \right] d\xi - \frac{1}{w} \int_0^\ell \exp \left[-w \int_\xi^\ell \frac{du}{\lambda(u)} \right] d\xi \quad (\text{C-12})$$